

First-year overwinter mortality in Eurasian perch (*Perca fluviatilis* L.)

Results from a field study and a simulation experiment

Radke R.J., Eckmann R. First-year overwinter mortality in Eurasian perch (*Perca fluviatilis* L.). Results from a field study and a simulation experiment.

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Abstract – The importance of overwinter mortality of 0+ perch (*Perca fluviatilis* L.) in central European lakes was estimated using a stochastic simulation model. The probability of overwinter mortality of a perch cohort was calculated by using a model developed for yellow perch (*P. flavescens* Mitchell). Winter duration from a long-term data set and the length of perch at the end of the first year from five lakes were used as input data. After 1000 simulation runs, the total extinction of a cohort in the lakes studied was never predicted. Mortality rates of more than 0.5 were only predicted in two of the five lakes, and rates of more than 0.3 in these two lakes were predicted in approximately 10% of all cases. For two consecutive winters differing in duration, the length-frequency distributions of 0+ perch in the autumn and following spring were compared by a graphical method. No significant size-dependent mortality of smaller individuals could be detected in any of the populations studied. Simulated spring length-frequencies were derived from observed autumn length distributions by the same model that was used for the stochastic simulation. These simulated and the empirical spring length-frequency distributions were not identical. The differences between the two distributions were attributed to growth, which occurred between the sampling dates. The results from the simulation and the analysis of the empirical data suggest that high overwinter mortality caused by starvation is rare in central European lakes.

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

There is conclusive evidence from field and laboratory studies that size-dependent overwinter mortality of early life stages can have a significant effect on year-class-strength of centrarchids, percids and percichthyids in temperate zones (Toneys & Coble 1980; Post & Evans 1989a; Johnson & Evans 1990, 1991; Byström et al. 1998). This mortality might be caused by starvation resulting from the physical conditions, such as water temperature and

winter duration, and the physiological condition of the fish (Toneys & Coble 1980; Post & Evans 1989a; Johnson & Evans 1996; Kirjasniemi & Valtonen 1997), by predation by other species or older conspecifics (Post & Evans 1989b; Miranda & Hubbard 1994), or by both factors. In either case, smaller individuals suffer higher mortalities compared to larger ones and year-classes with a small mean size at the end of the first growing season suffer higher mortality than those with a large mean size. A study by Nielsen (1980), for example,

showed that a high amount of year-to-year variability in the year-class strength of yellow perch (*P. flavescens* Mitchell) could be explained by incorporating the length of 0+ fish at the end of the year as a variable in a multiple regression model. Craig (1982) and Craig & Kipling (1983) did not directly use first-year growth as a variable in their multiple regression model but were able to explain a significant amount of the variability in Eurasian perch (*P. fluviatilis* L.) recruitment by using water temperature (accumulated degree-days above 14°C) throughout the first summer of life as a variable. This variable correlated positively with mean length at the end of the first year.

From laboratory experiments, Post and Evans (1989a) developed a bivariate model that predicted the probability of overwinter starvation mortality of 0+ yellow perch by incorporating total length and winter duration as variables. This model was then tested successfully on empirical data. Within the same study, stochastic simulations using varying mean lengths and winter durations from a range naturally occurring in Canadian lakes showed that overwinter mortality can substantially influence first year recruitment success. A recently published study by Byström et al. (1998) was the first evidence showing overwinter mortality of 0+ Eurasian perch to be of importance in four small boreal lakes situated in central Sweden. Thus, the aim of the study presented here was to evaluate the extent to which overwinter starvation might influence mortality and thus first-year recruitment of Eurasian perch under the climatic conditions of central Europe. First, the range and variability of overwinter mortality of perch is estimated by a stochastic simulation incorporating the model of Post & Evans (1989a). Length measurements of 0+ perch at the end of the first year and winter durations from five central European lakes were used as input data for these simulations. Both yellow and Eurasian perch are very similar in all aspects of their biology (Thorpe 1977), and thus Post and

Evans' model can be applied to data of Eurasian perch. Secondly, empirical autumn length frequency distributions of 0+ perch from these lakes are compared with empirical spring distributions to find indirect evidence for overwinter mortality. Finally, non-empirical spring length-frequency distributions, which were derived from the application of the Post and Evans probability model of overwinter mortality due to starvation on the autumn distributions (henceforth referred to as "modelled" distributions), are compared with the empirical autumn length distributions used for the calculation. It is hypothesized that overwinter mortality detected by the comparison of the empirical autumn distribution with the empirical spring distribution but not by the comparison of the modelled distribution with the empirical one would be evidence for size-selective predation on the 0+ perch.

Material and methods

Study area and sampling

Five natural lakes, situated in northeastern Germany, were chosen for this study (Table 1). The lakes are similar in concentrations of total phosphorous, chlorophyll-a, total dissolved solids and fish species composition (Eckmann 1995). Perch of 0+ years were caught either with a beach seine (30 m long, 4-mm bar mesh) or by electric fishing (EFKO: 7 kW, 300–600 V, DC), if lake topography did not permit the use of a beach seine. For the 1994 year-class, fish were caught from 10 to 14 October 1994 and from 11 to 19 April 1995 and for the 1995 year-class from 10 to 18 October 1995 and from 15 to 23 April 1996. All fish were measured to the nearest millimeter (total length). Lake temperatures were measured continuously with temperature loggers at three depths (1 m, 3 m and 5 m) in Kleiner Döllnsee from April to October in 1994 and 1995. Additionally, mid-lake temperature profiles were taken monthly from March to Octo-

Table 1. Location, morphometric and limnological characteristics of the study lakes. Total dissolved solids and chlorophyll-a values are means from 2–3 epilimnetic measurements during summer stratification. Total-P are means from measurements after spring mixis in 1995 and 1996. All parameters except location and phosphorous concentration are taken from Eckmann (1995).

	Kleiner Döllnsee	Großer Vätersee	Kleiner Vätersee	Redernswalder See	Werbellinsee
Location					
longitude,	13°35'E	13°33'E	13°34'E	13°52'E	13°42'E
latitude	52°59'N	53°00'N	53°01'N	53°03'N	52°50'N
Area (km ²)	0.24	0.12	0.09	0.53	8.04
Maximum depth (m)	8	13	14	12	54
Total dissolved solids (mg/l)	236	200	164	199	250
Chlorophyll-a (µg/l)	9.8	4.2	2.8	8.8	4.7
Total-P (µg/l)	29	22.5	27.5	30	53

ber in every lake in both years. Oxygen concentration was sufficient for perch survival at low temperatures (Petrosky & Magnuson 1973) down to a depth of 4 m on 2 February and 14 April in 1996 in Kleiner Döllnsee. Oxygen concentration was measured at these dates because all lakes were completely covered with ice from mid-November 1995 to mid-April in 1996 and winterkill due to insufficient oxygen saturation might have influenced the results of the study. None of the lakes was covered with ice for more than two weeks during the winter of 1994/1995.

Variability of size-dependent overwinter starvation mortality in perch populations

By applying the model developed by Post & Evans (1989a), the probability of overwinter starvation mortality (PMORT) for yellow perch can be estimated as a function of their total length (TL in mm) in autumn and the winter duration (WD: defined as the number of days that epilimnic water temperature was $\leq 6^{\circ}\text{C}$) in days. As no long term data of winter duration of our study lakes were available, water temperature data from Müggelsee (location: long. $13^{\circ}38'\text{E}$, lat. $52^{\circ}27'\text{N}$, area: 7.7 km^2 , maximum depth: 8 m) were used to determine the beginning and end of the winter period. Mean temperature difference (April 1994–1996, October 1994–1995, 1 m depth, $n=8$) between Kleiner Döllnsee and Müggelsee was -0.17°C ($\text{SD}=0.69^{\circ}\text{C}$) and was not significantly different from 0 ($t=-0.73$, $P>0.05$). Mean winter duration for Müggelsee was 144 days ($\text{SD}=11\text{ d}$, $n=20$) for the period of 1976–1996.

Both summers of 1994 and 1995 had significantly higher accumulated degree days, above 14°C epilimnic water temperature in Lake Müggelsee (3011 and 3336), than the average summer 1976–1995 (Mean=2631, $\text{SD}=278$, $t=-6.1$, $P<0.001$). This might have caused increased first year growth of perch in our study lakes. Thus, using the mean autumn lengths of 0+ perch for these two years as input data might have biased the results of the

simulation. No data were available for mean autumn lengths of 0+ perch before 1994, so perch from gillnet catches were used to back-calculate mean lengths from opercular bones for the years 1988–1992 (Table 2, data from Radke, 1998). The mean accumulated degree days for these 5 years were 2678 ($\text{SD}=117$), which was not significantly different from the mean of the remaining years (mean=2616, $\text{SD}=316$, $t=-0.4$, $P>0.05$).

The simulation included four steps: i) 1000 winter durations were randomly selected from a normal distribution of Müggelsee data (144 days, $\text{SD}=11$), ii) 1000 autumn mean total lengths for each lake were randomly selected from a normal distribution with lake-specific mean and standard deviation for the years 1988–1992, iii) an autumn length-frequency distribution of 100 individuals was created by randomly selecting from a normal distribution with the mean created in step ii and the same standard deviation, and iv) for each lake overwinter mortality for a cohort of 100 individuals was calculated for 1000 pairs of the randomly selected winter durations and autumn length-frequency distributions.

Comparison of autumn and spring length-frequency distributions

To detect the effect of size-dependent mortality on a length-frequency distribution, empirical quantile-quantile (QQ) plots were used (Chambers et al. 1983). This method permits the comparison of two distributions by describing their shapes with quantiles. The autumn and spring distributions were transformed to quantile distributions (quantiles 1, 5, 10, 25, 50, 75, 90, 95, 99). The incremental differences between the lengths of spring and autumn quantiles were then plotted versus the corresponding autumn quantiles. The regression slope of this plot was tested for significant difference from zero at the $P<0.05$ level. Overwinter mortality of smaller individuals is indicated by a negative slope and positive increment values.

To compare empirical increment plots and plots

Table 2. Back-calculated mean lengths (\bar{x} , total length, mm), standard deviation (SD) and number (n) of 0+ perch for which length was back-calculated in 1988–1992 (rounded values). No data were available for Kleiner Döllnsee in 1988. Data are modified from Radke (1998).

Year Lake	1988			1989			1990			1991			1992			1988–1992	
	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD
Großer Vätersee	69	9	6	65	6	17	64	5	11	71	5	11	66	6	27	67	6
Kleiner Döllnsee	–	–	–	68	6	7	70	10	12	71	6	10	71	6	32	70	7
Kleiner Vätersee	71	7	6	72	6	3	68	4	5	62	6	13	68	10	4	68	7
Redernswalder See	73	7	7	69	8	4	74	7	16	73	7	12	73	5	18	72	7
Werbellnsee	78	8	15	79	9	22	75	6	25	73	5	18	74	7	18	76	7

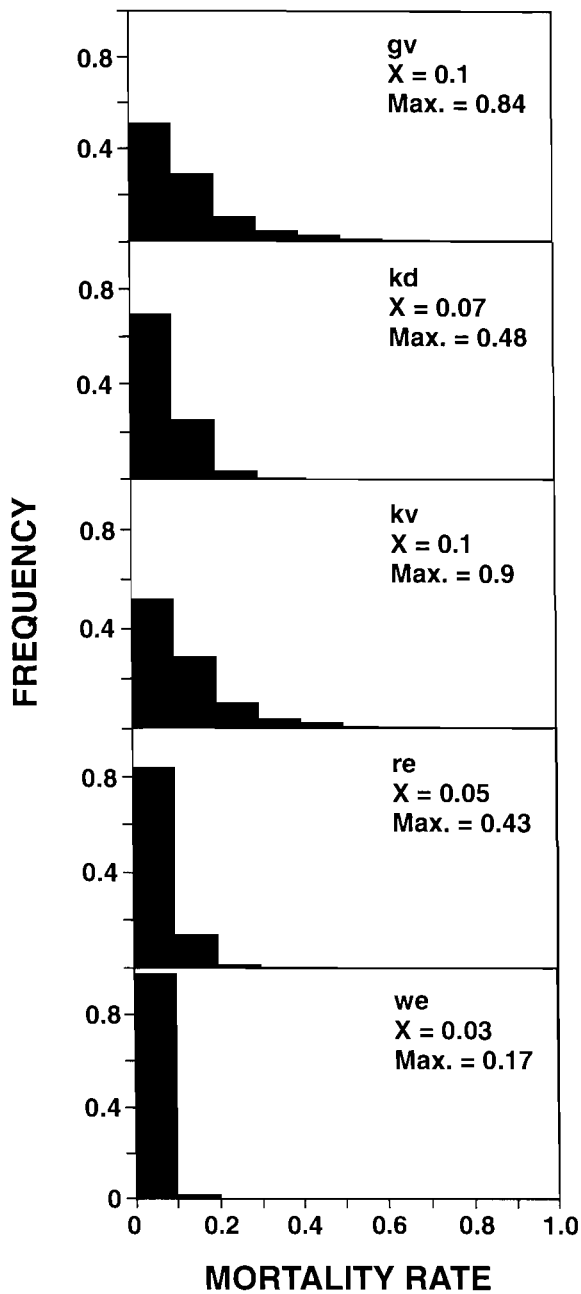


Fig. 1 Predicted frequency distributions of overwinter mortality rate of perch cohorts from 1000 runs based on simulated length-frequency distributions and winter durations. The simulation used lake-specific mean total lengths and standard deviations. Mean winter duration and standard deviation were taken from data of Müggelsee. Median (X) and maximum value of simulated overwinter mortality are indicated for each lake.

derived from modelled spring distributions the probability of mortality (PMORT) was calculated for all mm length classes from the empirical autumn length-frequency distributions of 0+ perch. Winter duration in all lakes was 138 days for winter 1994–1995 and 152 days for winter 1995–1996. Increment

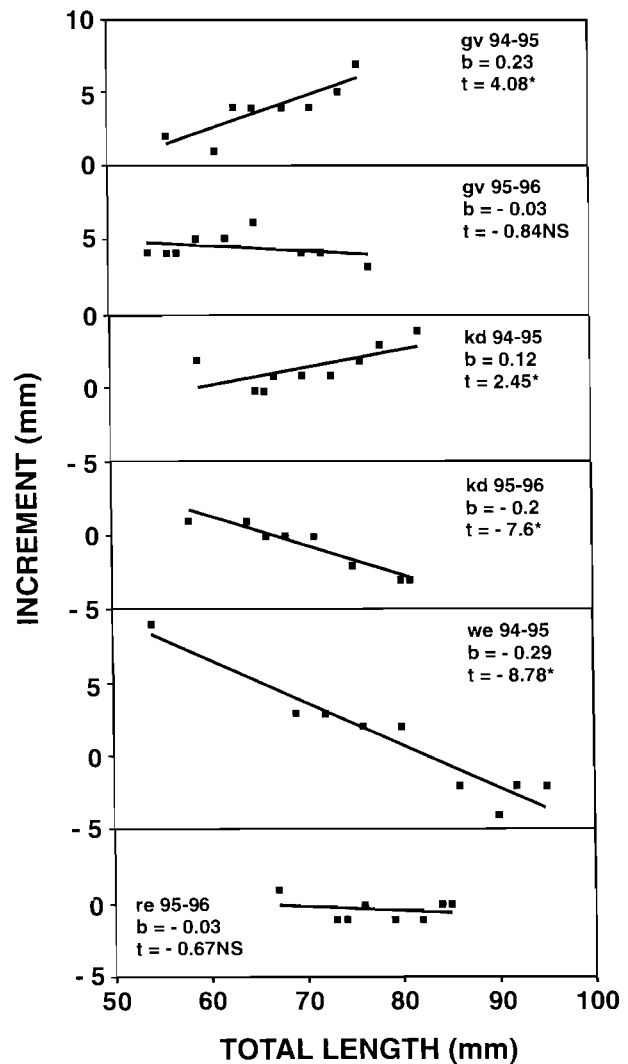


Fig. 2. Increment plots for perch in winter 1994–1995 and 1995–1996. Slopes and two-tailed t-test values for $H_0: b=0$ are indicated. Significant ($P<0.05$) slopes are indicated by*. Note that y-axis intervals are not identical in all single plots. gv (Großer Vätersee), kd (Kleiner Döllnsee), re (Redernswalder See), we (Werbellinsee).

plots were then constructed from the autumn and the simulated spring length-frequency distributions.

Results

Variability of size-dependent overwinter starvation mortality in perch populations

Simulated overwinter mortality of a 0+ perch cohort caused by starvation never exceeded 0.9 for all lakes studied (Fig. 1). Mortality rates above 0.5 were only observed in Großer and Kleiner Vätersee. In both lakes mortality rates >0.3 were observed in approximately 10% of all cases (less than two percent in the other lakes). Lowest median an-

nual mortality rate was 0.03 in Werbellinsee and highest was 0.1 in Großer and Kleiner Vätersee.

Comparison of autumn and spring length-frequency distributions

All slopes of the perch increment plots calculated with the data of winter 1994–95 were significantly different from zero (Fig. 2). In the case of Großer Vätersee and Kleiner Döllnsee, the slope was positive and increment values were >0. This suggests that there was no size-selective mortality but that growth of larger individuals occurred in both lakes. Alternatively, both size-selective mortality and growth of larger individuals might have occurred simultaneously. The increment plot of Werbellinsee indicated higher mortality of larger individuals. As some of the increment values were positive, the fish must have increased in length between the sampling dates. Catch data from Kleiner Vätersee and Redernswalder See were not sufficient to create autumn and spring length-frequency distributions in 1994–1995 (Table 3).

The slopes of the increment plots for 1995–1996 were all negative, but only in the case of Kleiner Döllnsee was the slope significantly different from zero. As in the case of Werbellinsee in 1994–1995, increment values were negative for the largest individuals. In contrast to the perch of Kleiner Döllnsee and Redernswalder See, those of Großer Vätersee increased in size from autumn to spring. This happened despite similar temperature regimes and little difference in sampling dates. Sample sizes from Kleiner Vätersee and Werbellinsee were not sufficient to create autumn and spring length-frequency distributions in 1995–1996.

Comparison of empirical increment plots and plots derived from modelled spring distributions

Slopes of the increment plots derived from empirical autumn and modelled spring length-frequency distributions were not significantly different from zero, except for Kleiner Döllnsee 1995–96 (Fig. 3). However, the slope of this increment plot was very close to zero and indicated that only a small proportion of the smaller individuals had suffered overwinter mortality.

The comparison of empirical increment plots (Fig. 2) with those derived from modelled spring distributions showed that only the Redernswalder See 1995–96 plots were similar. In all other cases increment values and slope signs of the empirical plots were different from those predicted by the simulated plots, indicating that the perch had grown between the sampling dates. This growth

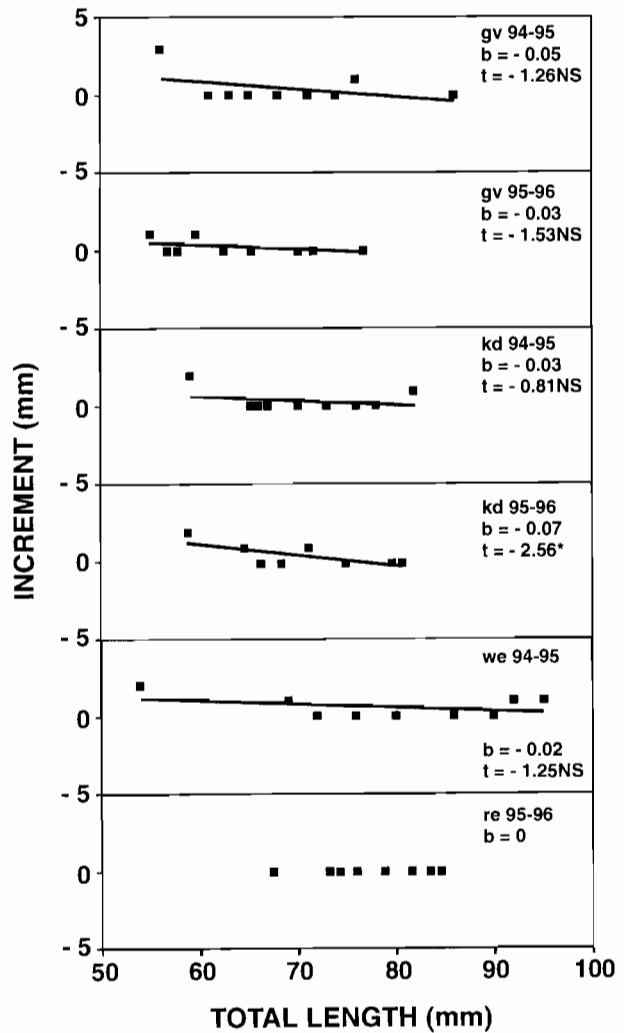


Fig. 3. Increment plots from empirical autumn and modelled spring length-frequency distributions for perch in winter 1994–1995 and 1995–1996. Slopes and two-tailed *t*-test values for $H_0: b=0$ are indicated. Significant ($P<0.05$) slopes are indicated by*. Abbreviations of lakes as in Fig. 2.

was generally size-dependent, with the exception of Großer Vätersee 1995–96.

Discussion

The results of the present study could not find direct evidence for size-selective overwinter mortality of small individuals in 0+ perch cohorts from the lakes studied. This was confirmed by the results of the simulation using input values from a larger data set. The unexpected size-selective mortality of larger individuals found in some of the cases was not likely to be a result of starvation. Size-selective gear (beach seine) enabling larger individuals to escape with higher probability during the spring sampling, might explain these findings. None of

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Table 3. Mean total lengths (\bar{x} , mm, rounded values), length range and number of 0+ perch caught per lake and season

Lake	Autumn 1994			Spring 1995			Autumn 1995			Spring 1996		
	\bar{x}	range	<i>n</i>	\bar{x}	range	<i>n</i>	\bar{x}	range	<i>n</i>	\bar{x}	range	<i>n</i>
Großer Vätersee	68	56–86	109	72	58–86	46	62	54–77	120	67	58–83	182
Kleiner Döllnsee	70	59–86	193	72	60–86	122	72	58–85	90	71	59–84	173
Kleiner Vätersee	–	–	–	–	–	–	–	–	–	84	82–85	5
Redernswalder See	77	75–79	7	–	–	–	79	67–87	82	77	68–86	48
Werbellinsee	80	52–96	204	81	62–95	167	80	76–83	9	–	–	–

these cases, though, indicated higher mortality of smaller individuals. However, despite the results of this study, first year overwinter mortality seems to be the most important factor restricting the northern distribution of fishes in North America and Eurasia. For example, Johnson & Evans (1990) showed that the stepwise invasion of the Laurentian Great Lakes by the white perch (*Morone americana* (Gmelin)) coincided with warmer-than-average summer and winter mean air temperatures during the late 1940s. The most northern extant populations are characterised by high overwinter mortalities of 0+ fish in cold winters. Byström et al. (1998) found size-dependent overwinter mortality to be very important in their lakes studied in the winter of 1994/1995. Growth season in these unproductive boreal lakes was restricted to a short period and as a consequence the mean size range of 0+ perch caught in autumn was approximately 40–55 mm. In a study presented by Shuter & Post (1990), the northern distributional limits of yellow and Eurasian perch could be explained by incorporating environmental and physiological variables in a multivariate model. Variation of food availability in this model leads not only to shifts of these limits, but also defines the border of the geographical zones where winter starvation begins to influence population structure. Shuter & Post (1990) determined such a border (about 50°N in western Canada) for the North American continent but not for Eurasia. It is noteworthy though that the study lakes of Post & Evans (1989a), in which size-selective overwinter mortality was significant, were south of this border (43–45°N).

An overview of first year growth of perch given in Thorpe (1977) and the results of this study (Tables 3 and 4) show that mean length after the first summer varies greatly even within regions of similar climate. While long-term studies in one lake identified summer temperatures to be the most important factor governing growth of 0+ perch (e.g. Le Cren 1958; Craig & Kipling 1983; Mooij et al. 1994), comparisons of first-year growth between different lakes or sites within a very large lake suggest that other factors such as

lake trophy (Hayward & Margraf 1987), food supply (Post & McQueen 1994) or intraspecific competition (Henderson 1985) explain more of the encountered interannual variance in growth. Both intra- and interspecific competition can lead to reduced growth of perch, as positive growth responses after massive fish removals (Persson 1986) and enclosure experiments with varying fish densities have shown (Hanson & Leggett 1985; Persson & Greenberg 1990a, b). This temperature independent variability of first year growth was probably underestimated in the model of Shuter & Post (1990). Therefore it is likely that resource limitation, which resulted in smaller than average autumn mean lengths, accounted for the observed but not predicted (by Shuter & Post (1990)) overwinter mortality in Post & Evans' (1989a) study.

To test whether the differences in climate between western Canada and central Europe would account for the greater effects of overwinter mortality found in the Canadian lakes a simulation for a lake of each region was performed using the same methods as mentioned above. Input data were the mean winter duration of Lake St. George (154 days, *n*=6, SD=8 days) and of Müggelsee (144 days, *n*=20, SD=8 days) and a mean cohort total length of 65 mm (SD=8 mm). This simulation only produced a difference of 0.04 between the two median values of cohort mortality rate (0.18 and 0.14), which clearly demonstrates that shorter winter duration in central Europe cannot serve as a simple explanation for higher overwinter survival. Although no fish were caught for food analysis during the winter in our study, there is a strong likelihood that the perch had consumed sufficient amounts of food to support their maintenance metabolism at low temperatures and thus avoided starvation. This is further confirmed by the differences between the empirical and the simulated increment plots, which can be explained best by size-dependent growth, which must have occurred between the sampling dates. As day-length during winter is inversely related to latitude, this factor is unlikely to have had a positive effect on food intake rates of 0+ perch in our study lakes.

as these are located 8–10° farther north than the lakes studied by Post & Evans (1989a). Light penetration in the Canadian lakes though might have been limited through longer lasting and thicker ice and snow cover (mean duration of ice cover on Müggelsee was 59 days (SD=36 days) for period 1978–1997 and 119 days (range 0–252 days) for a set of summer-stratified lakes ($n=41$) in continental North America (Shuter, Schlesinger & Zimmerman 1983)), which sets constraints on the foraging ability of an optically oriented predator such as the perch (Bergman 1988).

Apart from starvation, predation by piscivorous fish might also have a great influence on the size and structure of a cohort of prey fish (Nielsen 1980; Post & Prankevicius 1987; Post & Evans 1989b). All lakes in this study have piscivorous perch populations, where the degree of piscivory is positively related to fish size and during summer perch regularly feed on juvenile perch (Radke, 1998). The simultaneous occurrence of starvation and predation mortality during winter would have been difficult to analyze. The lack of evidence for size-selective mortality of smaller individuals, though, suggests that either predation pressure during winter was low or less probable in the case of perch, as predator and predation were not size-selective. Abundance estimates before and after winter might have produced data supporting the latter assumption, but were not feasible within the scope of this study. Thus, we conclude that size-selective overwinter mortality of smaller 0+ individuals due to starvation does not seem to be a major factor structuring perch populations in lakes under the climatic conditions of central Europe and hence is expected to be observed in Eurasia only in regions with more severe winter conditions (i.e., higher altitudes or latitudes).

Resumen

1. En cinco lagos de Europa central, estimamos la importancia de la mortalidad invernal de individuos de edad 0 de *Perca fluviatilis*, con un modelo de simulación estocástica. Utilizamos como variables la duración del invierno (número de días en los que la temperatura epilimnica fue $\leq 6^{\circ}\text{C}$) y el crecimiento durante el primer año de vida y calculamos la probabilidad de mortalidad usando un modelo desarrollado para *P. flavescens* Mitchill. Sólo en dos de los lagos encontramos tasas de mortalidad superiores a 0.5.

2. En dos inviernos consecutivos de diferente duración e intensidad, comparamos las distribuciones de frecuencia de longitud, primavera y otoño, de los individuos de edad 0 con un método gráfico. En ninguna de las poblaciones estudiadas encontramos mortalidades dependientes del tamaño en los peces más pequeños.

3. Frecuencias no empíricas de longitudes primaverales se obtuvieron a partir de las frecuencias de longitudes observadas en otoño con la simulación estocástica, y encontrando que éstas no fueron idénticas a las empíricas. Atribuimos las diferencias

observadas entre las dos distribuciones al crecimiento de los individuos entre las fechas de muestreo.

4. Los resultados obtenidos por simulación y los datos empíricos sugieren que la mortalidad invernal por inanición es poco frecuente en lagos centroeuropeos y que sólo tendría efectos sobre las poblaciones de *P. fluviatilis* a latitudes o altitudes mayores.

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